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Editorial: Roles and regulatory mechanisms of ABA in plant development

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Editorial on the Research Topic

Roles and regulatory mechanisms of ABA in plant development

As a sesquiterpene phytohormone derived from epoxy-carotenoid cleavage, abscisic acid (ABA) is extensively involved in the regulation of various plant growth processes as well as adaptive responses to biotic and abiotic stresses (Nambara and Marion-Poll, 2005; Hirayama and Shinozaki, 2007; Yoshida et al., 2014; Wang et al., 2020). In this special issue “*Roles and Regulatory Mechanisms of ABA in Plant Development*”, 4 articles were published that explore ABA involvement in different developmental processes, covering outstanding advances in the fundamental roles of ABA in diverse plant research fields.

Previously, important functions of ABA biosynthetic pathways have been deciphered through molecular-genetic, biochemical, and pharmacological approaches (Koornneef et al., 1982; Giraudat et al., 1992; González-Guzmán et al., 2002). A core signaling module involving “PYR/PYL/RCAR-PP2C-SnRK2-AREB/ABF” has been proposed and experimentally validated to play key roles in plant ABA signaling (Ma et al., 2009; Cutler et al., 2010). In the ABA signaling pathway, ABA is first recognized by the receptor proteins PYRABACTIN RESISTANCE (PYR)/PYR1-LIKE (PYL)/REGULATORY COMPONENTS OF ABA RECEPTORS (RCAR), and then interact with the clade A protein phosphatases of type 2Cs (PP2Cs). PP2Cs inactivation releases the inhibition on Sucrose non-fermenting 1-related protein kinases 2 (SnRK2) protein kinases that phosphorylate downstream ABA-responsive element binding factors (ABFs) to modulate ABA responses (Fujii et al., 2009; Park et al., 2009; Chen et al., 2020).

As the core element in ABA signaling pathway, PYR/PYL/RCAR family has been reported to play essential roles (Park et al., 2009). A recent study by Shang et al. identified novel pathways to modify ABA signaling through PYR1. In Arabidopsis, Brassinosteroid-Insensitive1-Associated Receptor Kinase1 (BAK1) interacts with PYR1 and phosphorylates PYR1 at the T137 and S142 sites. Phosphorylated PYR1 mainly exists in a monomeric form and increases the degree of complex formation with ABI1 and the ABA binding capacity. New findings presented in this issue by Shang et al. demonstrated that in addition to BAK1 interaction with OST1, importantly BAK1 also positively modulates ABA signaling through interaction with PYR1. This research further expanded our knowledge of the ABA signaling pathway.

The plant cell wall is structurally complex and pectin is a major component of it (Klis et al., 2006). When plant cells encounter stress, cell wall key components, such as pectin, pectin methylesterase (PME), and apoplastic Ca²⁺ will be reconstructed (Hamann et al., 2009; Wu et al., 2010). Wu et al. identified and characterized an Arabidopsis type-II PME gene *PME53*, which encodes a cell wall deposited protein and is highly expressed in guard cells as an abscisic acid (ABA)-regulated gene. They found that *PME53* regulates the activity of the core stomatal transcription factors SCRM and MUTE to modulate the development of stomatal and the flexibility of guard cell wall, thereby enhancing the adaptation of Arabidopsis to temperature changes. This research provided a novel perspective on ABA-mediated adaptive response of plant cell development to environmental stress.

In addition to key functions in stress response, ABA is also involved in several other important physiological processes in plants including seed maturation. Gupta et al. reviewed that ABA plays a key role in fruit development and ripening. In the later fruit ripening stage, the export of phloem ABA was decreased significantly, and ABA accumulation occurred. The interaction of ABA with ethylene and other plant hormones may play an essential role in fruit growth and ripening.

Plants also use complex signaling systems regulated by light and abscisic acid (ABA) components to optimize growth and development in different situations. Plants might reduce CO₂ entry into leaves and limit photosynthesis by controlling stomatal aperture in response to stress conditions (Dong et al., 2015; Kuromori et al., 2018; Yoshida et al., 2019). However, it is still a mystery that how ABA and light signals are integrated at the molecular level? ABI5 (Abscisic acid-insensitive 5) is a key signaling hub in the ABA pathway. When plants sense the ABA signal, SnRK2 protein kinases activate the ABI5 subfamily proteins to promote the expression of ABA-responsive genes (Furhata et al., 2006; Umezawa et al., 2009). Recent in silico analysis of the public datasets performed by Bulgakov and Koren found that ABI5 is a main player that links ABA and light signaling during plant

development. It is important to understand the interactions of ABA and light signals to improve the photosynthetic efficiency of crops, especially under climate challenged growth conditions.

Altogether, the contributions published in this special issue captured latest excellent advances providing new insights into ABA regulation of plant growth and development. The new research findings reported by Shang et al. and Wu et al. revealed novel components or pathways involved in ABA signaling. Light is an essential signal that regulates the physiological cycle, basic photomorphogenetic pathways, and secondary metabolites of plants (Chen et al., 2004). However, the role of abscisic acid (ABA) signaling in light response is still poorly understood. Bulgakov and Koren and Gupta et al. systematically reviewed the network between ABA and light signals or other phytohormones in the regulation of plant developmental programs. Together, in view of these research advances, future prospects targeting ABA signaling pathway through different strategies to regulate plant growth and development especially under a range of environmental challenges are very promising. We wish to thank all the authors for their contributions and the reviewers for their critical assessments of these articles. We also thank the *Frontiers in Plant Science* for giving us the opportunity to serve as guest editors of the Research Topic “Roles and Regulatory Mechanisms of ABA in Plant Development”.

Author contributions

All the authors participated in the editing of this Research Topic. GL wrote the draft, and all the other authors provided suggestive comments on the editorial. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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References

- Chen, M., Chory, J., and Fankhauser, C. (2004). Light signal transduction in higher plants. *Annu. Rev. Genet.* 38, 87–117. doi: 10.1146/annurev.genet.38.072902.092259
- Chen, K., Li, G., Bressan, R., Song, C., Zhu, J., and Zhao, Y. (2020). Abscisic acid dynamics, signaling, and functions in plants. *J. Integr. Plant Biol.* 62, 25–54. doi: 10.1111/jipb.12899
- Cutler, S., Rodriguez, P., Finkelstein, R., and Abrams, S. (2010). Abscisic acid: emergence of a core signaling network. *Annu. Rev. Plant Biol.* 61, 651–679. doi: 10.1146/annurev-arplant-042809-112122
- Dong, T., Park, Y., and Hwang, I. (2015). Abscisic acid: biosynthesis, inactivation, homeostasis and signalling. *Essays. Biochem.* 58, 29–48. doi: 10.1042/bse0580029
- Fujii, H., Chinnusamy, V., Rodrigues, A., Rubio, S., Antoni, R., Park, S., et al. (2009). *In vitro* reconstitution of an abscisic acid signalling pathway. *Nature* 462, 660–664. doi: 10.1038/nature08599
- Furihata, T., Maruyama, K., Fujita, Y., Umezawa, T., Yoshida, R., Shinozaki, K., et al. (2006). Abscisic acid-dependent multisite phosphorylation regulates the activity of a transcription activator AREB1. *Proc. Natl. Acad. Sci. U.S.A.* 103, 1988–1993. doi: 10.1073/pnas.05056671
- Giraudat, J., Hauge, B., Valon, C., Smalle, J., Parcy, F., and Goodman, H. (1992). Isolation of the arabidopsis ABI3 gene by positional cloning. *Plant Cell* 4, 1251–1261. doi: 10.1105/tpc.4.10.1251
- González-Guzmán, M., Apostolova, N., Bellés, J., Barrero, J., Piqueras, P., Ponce, M., et al. (2002). The short-chain alcohol dehydrogenase ABA2 catalyzes the conversion of xanthoxin to abscisic aldehyde. *Plant Cell* 14, 1833–1846. doi: 10.1105/tpc.002477
- Hamann, T., Bennett, M., Mansfield, J., and Somerville, C. (2009). Identification of cell-wall stress as a hexose-dependent and osmosensitive regulator of plant responses. *Plant J.* 57, 1015–1026. doi: 10.1111/j.1365-313X.2008.03744.x
- Hirayama, T., and Shinozaki, K. (2007). Perception and transduction of abscisic acid signals: keys to the function of the versatile plant hormone ABA. *Trends Plant Sci.* 12, 343–351. doi: 10.1016/j.tplants.2007.06.013
- Klis, F., Boorsma, A., and De Groot, P. (2006). Cell wall construction in *saccharomyces cerevisiae*. *Yeast* 23, 185–202. doi: 10.1002/yea.1349
- Koornneef, M., Jorna, M., Brinkhorst-van der Swan, D., and Karssen, C. (1982). The isolation of abscisic acid (ABA) deficient mutants by selection of induced revertants in non-germinating gibberellin sensitive lines of *arabidopsis thaliana* (L.) heynh. *Theor. Appl. Genet.* 61, 385–393. doi: 10.1007/BF00272861
- Kuromori, T., Seo, M., and Shinozaki, K. (2018). ABA transport and plant water stress responses. *Trends Plant Sci.* 23, 513–522. doi: 10.1016/j.tplants.2018.04.001
- Ma, Y., Szostkiewicz, I., Korte, A., Moes, D., Yang, Y., Christmann, A., et al. (2009). Regulators of PP2C phosphatase activity function as abscisic acid sensors. *Science* 324, 1064–1068. doi: 10.1126/science.1172408
- Nambara, E., and Marion-Poll, A. (2005). Abscisic acid biosynthesis and catabolism. *Annu. Rev. Plant Biol.* 56, 165–185. doi: 10.1146/annurev.arplant.56.032604.144046
- Park, S., Fung, P., Nishimura, N., Jensen, D., Fujii, H., Zhao, Y., et al. (2009). Abscisic acid inhibits type 2C protein phosphatases via the PYR/PYL family of START proteins. *Science* 324, 1068–1071. doi: 10.1126/science.1173041
- Umezawa, T., Sugiyama, N., Mizoguchi, M., Hayashi, S., Myouga, F., Yamaguchi-Shinozaki, K., et al. (2009). Type 2C protein phosphatases directly regulate abscisic acid-activated protein kinases in *arabidopsis*. *Proc. Natl. Acad. Sci. U.S.A.* 106, 17588–17593. doi: 10.1073/pnas.0907095106
- Wang, Y., Hou, Y., Qiu, J., Wang, H., Wang, S., Tang, L., et al. (2020). Abscisic acid promotes jasmonic acid biosynthesis via a 'SAPK10-bZIP72-AOC' pathway to synergistically inhibit seed germination in rice (*Oryza sativa*). *New Phytol.* 228, 1336–1353. doi: 10.1111/nph.16774
- Wu, H., Hsu, S., Luo, D., Chen, S., Huang, W., Lur, H., et al. (2010). Recovery of heat shock-triggered released apoplastic Ca²⁺ accompanied by pectin methylesterase activity is required for thermotolerance in soybean seedlings. *J. Exp. Bot.* 61, 2843–2852. doi: 10.1093/jxb/erq121
- Yoshida, T., Christmann, A., Yamaguchi-Shinozaki, K., Grill, E., and Fernie, A. (2019). Revisiting the basal role of ABA - roles outside of stress. *Trends Plant Sci.* 24, 625–635. doi: 10.1016/j.tplants.2019.04.008
- Yoshida, T., Mogami, J., and Yamaguchi-Shinozaki, K. (2014). ABA-dependent and ABA-independent signaling in response to osmotic stress in plants. *Curr. Opin. Plant Biol.* 21, 133–139. doi: 10.1016/j.pbi.2014.07.009